The Light Responses of *Tegula funebralis*

(Mollusca; Gastropoda)

BY

DOROTHEA F. KOSIN

Hopkins Marine Station of Stanford University,
Pacific Grove, California

(7 Text figures)

The behavior of *Tegula funebralis* (A. Adams, 1854) on the shore is complex. The snails are found clustered in cracks and crevices of rocks on both sunny and foggy days when the tide is low. Their movements in tidepools are inconsistent; sometimes all snails are gathered on the shady side, at others they are scattered throughout the pool. They are subjected to the action of waves and currents, as well as tidal exposure and submersion, at different light conditions over the tidal cycle. To establish the role of each factor (such as light) would be difficult in nature, but in the laboratory most of the other factors can be controlled and light varied.

METHODS

Tegula funebralis were tested for reactions to light in several manners: (1) Three aquaria, as much alike in contents as possible (rocks, shell fragments, algæ, number of snails) were set up under different light conditions and the snail movements noted. (2) Groups of snails were subjected to different intensities and spectral regions of visible light, and their reactions observed and timed. (3) Individuals were allowed to move in directional light. (4) Eyes and other appendages were removed and the response of such operated snails compared with the normal. Such operations were not generally harmful: all operated animals survived for at least two weeks and no infections were obvious. (Before operation, the snails were anesthetized by slow addition of an equal volume of isotonic $MgCl_2$ solution to sea water in which a number of snails were lying upside down. A temperature of 30° C also served to keep the snails extended out of their shells.)

RESULTS

(1) The experiments with 3 aquaria in different light conditions indicate that *Tegula funebralis* avoid light. Fig. 1 shows the number of snails at or near the surface of the water (all others being on or near the bottom). The day-night exposure shows great migration downwards during full daylight; the snails gather in the shadiest parts under algæ, behind rocks, on the shady side of the aquarium. In darkness (with only a dim ruby light for occasional observation), the snails all remained at water level all the time. Snails kept at a constant low light intensity (about 70 foot candles) tended to stay at the top, though somewhat less than those in complete darkness.

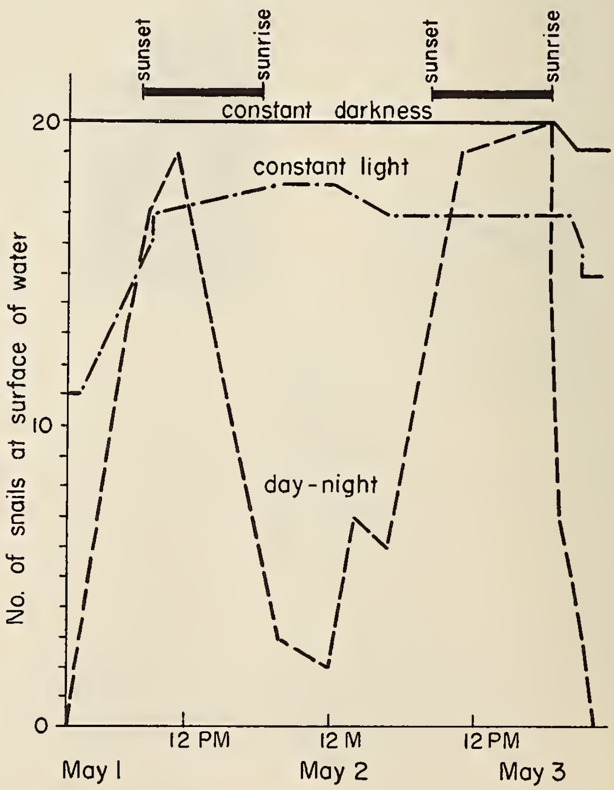

Figure 1: Distribution of 20 *Tegula funebralis* in each of three similar aquaria under different light conditions: normal day and night; constant illumination at 70 foot candles; and darkness.

In constant conditions the distribution of *Tegula funebralis* remains constant. When light conditions are alternated between light and dark the distribution alternates correspondingly up and down. (Fig. 2) The alternating light was presented out of phase with the day-night cycle and was conducted with snails which had been in the dark for two weeks. The response to the change of light conditions starts immediately, and the new distribution is reached within approximately one hour.

(2) Another method for measuring the light response was exposing groups of snails to beams of different inten-

Note: The following abbreviations are used where appropriate in all figures in this article.

a shell aperture	ht head tentacle
an anus	k kidney
cm columellar muscle	mc mantle cavity
ct ctenidium	op operculum
e eye	os osphradium
f foot	r rectum
g gonad	s shell
h heart	sc spiral caecum
st stomach	

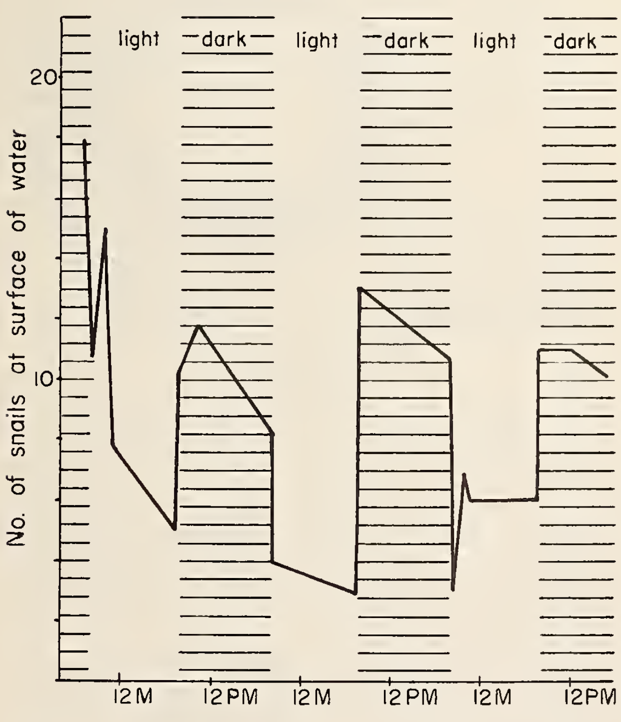

Figure 2: Effect of alternating light (70 foot candles) and darkness on 20 snails that had previously been in darkness for two weeks. The cycle is opposite to that of actual day and night.

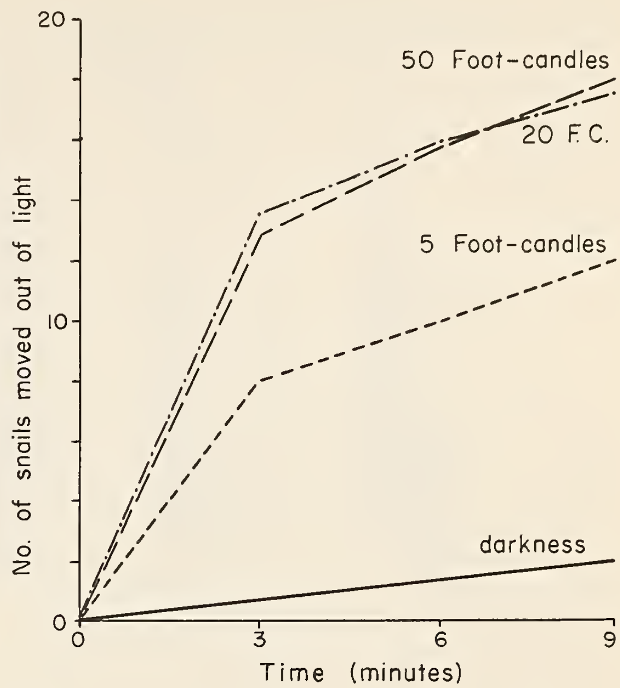

Figure 3: Rate of movement of snails out of a beam of light at three different intensities (5, 20, 50 f.c.). The rate in darkness is compared.

sities of light, and observing their rate of exit from the lighted area. As soon as the snails were placed in a circle of light, they began turning and pushing each other around in their attempt to move out of the light. They move to the darkest areas available, and rest only when they reach a crack or maximum darkness. The same number of snails left in the same area, but without light, disperse much more slowly. (Fig. 3). Snails previously adapted to different light intensities were also tested in this manner (Fig. 4). Those previously exposed to full sunlight (6000 F.C.) scarcely responded at all.

(3) Both operated and normal snails give a "shadow reaction," which is best observed if the snail is lying on its back, with foot partly extended. (If it is not extended far enough, it will withdraw into the shell when shadowed. If it is extended too far, the snail turns over and will not react at all. When the snail is attached to a surface by its foot, shading causes it to pull back its head, and to remain in that position for some time,— e. g. up to 5 minutes).

But when it is upside down, its normal reaction to a shadow is a slight contraction and pulling back of the foot, followed by a short period of quiet, and then a relaxation or extension of part or all of the foot. There is great variation in the *amount* of contraction, even in the same

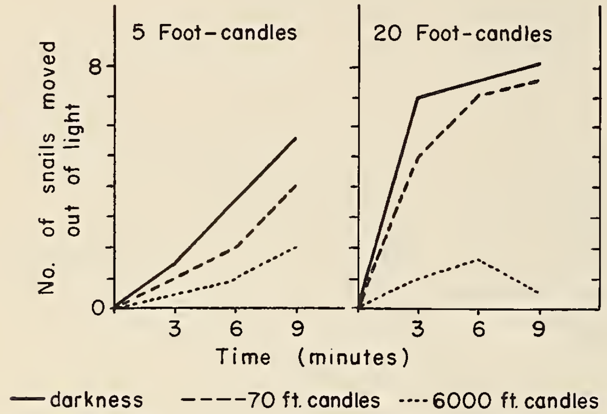

Figure 4: Rate of movement of snails out of a beam of light (5 and 20 foot candles), after previous adaptation to darkness, 70 foot candles and full daylight (6000 f.c.).

snail. The *duration* also varies, but not necessarily with the visible degree of contraction. A snail may contract deeply but shortly, or only slightly, but remain still for some time. Fig. 5 indicates the duration of contractions caused by 19 successive shadowings of 3 different snails; the average is 3 to 4 seconds. (The light was a microscope lamp about 30 cm above the snail, with some 7.5 cm of sea water to absorb much of the infra red. The visible intensity at the level of the snail was 20 F.C.)

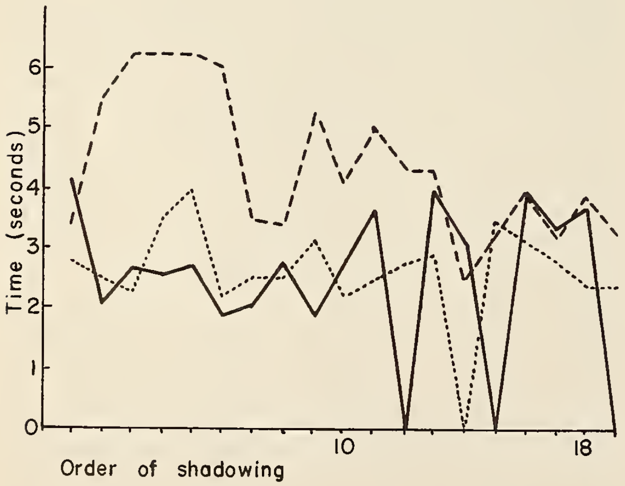

Figure 5: Duration of contraction reaction induced by 19 successive shadowings of three different snails (represented by solid, broken and dotted lines). Average duration, about 3.5 seconds (omitting the four failures, of zero durations). Light, 20 foot candles.

The same procedure was followed at different spectral regions isolated by glass filters; the intensities were adjusted to give about equal reading on a G. E. light meter, which approximates the human eye over much of the visible range. No significant difference in the duration of the response was noted to shading of either red, yellow, blue or green light (Fig. 6). However, in the far red light from a photographic ruby lamp (10 watts at 1 foot) no shadow response could be elicited.

A sudden illumination, even by bright light, does not cause such a consistent and quick reaction; it is the disappearance of light which causes the withdrawal. Nor does re-illumination visibly affect the total shadowing reaction. If a snail is left in darkness for over an hour, then put on its back, there may be a long contraction but this cannot be repeated as well as the shadow reaction. During the first minute or longer of such light exposure, the snail may be very insensitive to shadows. The amount of time

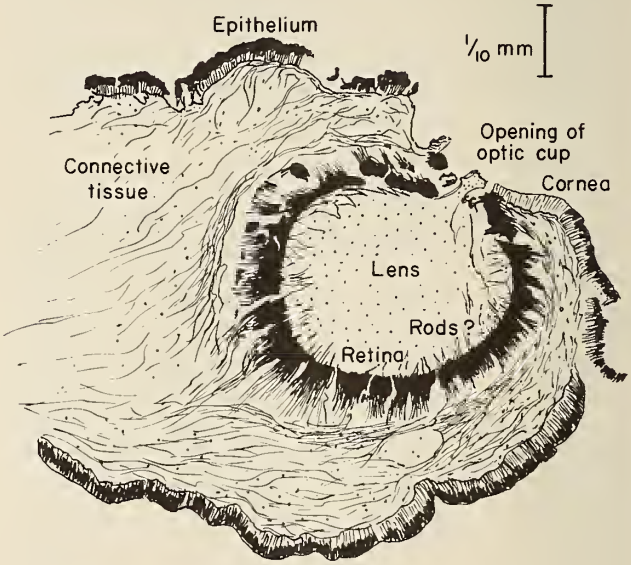

Figure 7: Sagittal section of the eye lobe of *Tegula funebralis,* about 25 microns thick.

necessary for this adaptation is dependent on the brightness of the light, and the intensity of light to which the snail had been exposed before the one hour dark period. Only when the snail becomes adapted to the new intensity will it react to shadows.

(4) In avoiding light, snails move to the closest dark area. In this they are aided by their eyes. A light directly above the snail causes it to move straight out of the light beam in any direction. If the left eye is removed the snail turns in about half a circle to the left before moving straight out of range of the light. Similarly a snail turns toward the

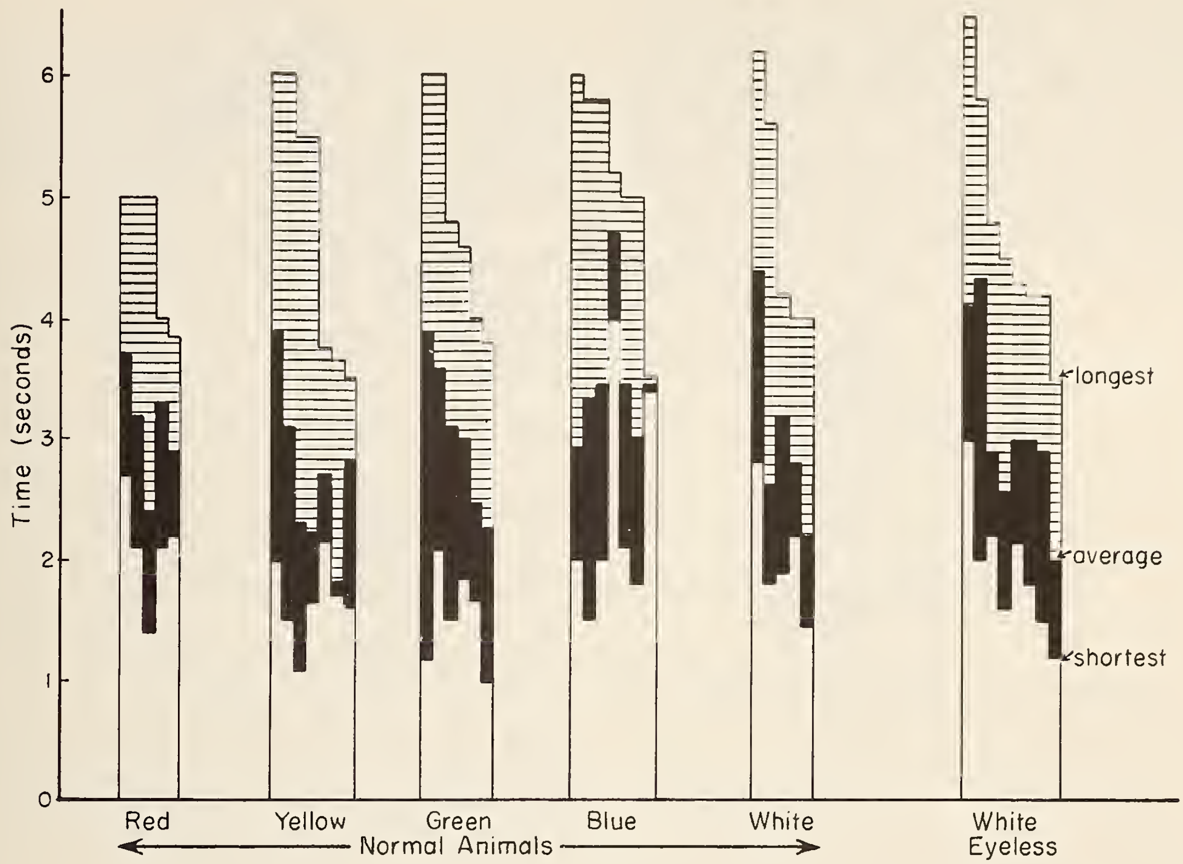

Figure 6: The effect of various spectral regions, and of white light, upon the shadowing response. The narrow columns represent different animals (5 to 8 in different histograms). Eyeless animals are shown in the last group. Intensities approximately equal, by G.E. photo-cell.

right when its right eye is removed. When both eyes are removed the snail generally turns around irregularly before leaving the lighted area.

In light from one side a normal snail moves away from the source with its head in its own shadow. The head turns from side to side, and each time that an eye is illuminated the snail turns back to its shadow or turns its head to the other side. In the same light an eyeless snail moves irregularly, even directly toward the light. Apparently it cannot distinguish direction without its eyes. A snail without its right eye will turn, usually toward the right, until its left eye is in shadow and then move directly out of the path of the light. When the left eye is removed the snail turns, usually to the left, until its right eye is in shadow before moving straight out of the beam of light.

Normal snails, snails without eyes, without epipodial tentacles and lobes, without propodial tubercles, and with none of these organs were tested for a shadow reaction. There was no difference in their reactions. Figure 2 shows the response of eyeless snails. Apparently the shadow reaction is more the result of a general body sensitivity, than of reception by a specific light sensitive organ.

These experiments indicate that the eyes are used for directional orientation in the light. It is the only function of the eye that I have been able to discover. The anatomy of the eye suggests this as well (Fig. 7). It is a simple, small ocellus containing a firm, clear substance which may correspond to a "lens". The small opening to the outside might function like a pin-hole camera, to form an image at the retina. Around the edge of the opening is a ring of unpigmented cells which might be a cornea. The retina appears to be formed by a direct invagination of the epidermis, continuous through the clear corneal area. The optic nerve branches proximal to the optic cup, sending fibers over its entire surface to connect with the retina.

The eyes of *Tegula funebralis* may represent a concentration of the same sensitive tissue present on the general body normally outside of the shell. The pigmentation of the retina resembles that of the epidermis, which contains melanin. Attempts to isolate a photosensitive pigment from the eyes, according to the recipe for squid retinas (Bliss, 1948) failed, probably because of the very small amount of tissue employed.

SUMMARY

Tegula funebralis is negatively phototactic. It becomes adapted to bright light, and loses its sensitivity temporarily. It has a general body sensitivity shown by a shadow reaction. Its eyes, simple lens ocelli, seem responsible for directional orientation to light. Without eyes its orientation is irregular.

LITERATURE CITED

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1948. The absorption products of visual purple of the squid and its bleaching products. Journ. Biol. Chem. **176**: 563 - 569

Observations on the Epipodium, Digestive Tract, Coelomic Derivatives and Nervous System of the Trochid Gastropod *Tegula funebralis*

BY

JOHN A. MACDONALD

AND

C. BURKE MAINO

Hopkins Marine Station of Stanford University,
Pacific Grove, California

(15 Text figures)

In spite of the abundance of *Tegula funebralis* (A. Adams, 1854) in the California intertidal, no account of its anatomy has yet appeared in the literature, although the anatomy of other trochids has been described (Randles, 1905; Fretter and Graham, 1962). To partially fill this void, a brief account of certain external and internal features of *T. funebralis* is herein presented.

The specimens of *Tegula funebralis* examined were collected at Mussel Point, Pacific Grove, California, during April and May, 1963. The animals were dissected alive after having been anesthetized with magnesium chloride; both frozen and paraffin sections were cut in order to make more detailed observations. Injection of suspensions of carborundum and carmine powders in sea water helped to determine the extent of specific body cavities. Both Mallory's connective tissue stain and Harris' hematoxylin produced excellent results after fixation with Bouin's fluid, made with seawater. A silver impregnation (Rowell, 1963) worked well for isolated nerves, but also stained muscle and connective tissue heavily in sections of the entire animal.

Epipodium: The epipodium of *Tegula funebralis* is composed of five elements: the neck lobes, anterior papillæ, epipodial tentacles, epipodial papillae, and epipodial ridges (Figures 1 and 2). On both sides of the animal the anterior quarter of the epipodium is occupied by the heavily ciliated neck lobe, which runs posteriorly from near the base of the optic peduncle. The border of